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Research Report

Remembering a Location Makes the Eyes Curve Away

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ABSTRACT—*Working memory is a system that keeps limited information on-line for immediate access by cognitive processes. This type of active maintenance is important for everyday life activities. The present study shows that maintaining a location in spatial working memory affects the trajectories of saccadic eye movements toward visual targets, as the eyes deviate away from the remembered location. This finding provides direct evidence for a strong overlap between spatial working memory and the eye movement system. We argue that curvature is the result of the need to inhibit memory-based eye movement activity in the superior colliculus, in order to allow an accurate saccade to the visual target. Whereas previous research has shown that the eyes may deviate away from visually presented stimuli that need to be ignored, we show that the eyes also curve away from remembered stimuli.*

In everyday life, people often make use of their ability to temporarily store information until a task is completed. Working memory is thought to underlie this ability. Baddeley and his colleagues (Baddeley, 1986; Baddeley & Hitch, 1974) proposed that working memory for visuospatial information is separated from working memory for verbal information. Furthermore, recent work by Awh and his colleagues (Awh & Jonides, 2001; Awh, Jonides, & Reuter-Lorenz, 1998) indicates that, at least for visuospatial memory, there is a close link between working memory and visual attention. They showed that when a location is kept in working memory, processing of stimuli at the memorized location is facilitated relative to processing of stimuli at other locations (Awh & Jonides, 2001), just as attending to a location improves the processing of information at that location (Posner, 1980). Conversely, when attention to memorized locations is interrupted, the ability to remember these locations is impaired (Awh et al., 1998). Brain-imaging studies confirm that rehearsal of spatial information modulates early sensory areas (Awh et al., 1999), and that the same fronto-parietal network is involved as in attention-related tasks (Kastner & Ungerleider, 2000).

These findings suggest a strong link between visuospatial working memory and spatial attention. In turn, an equally strong link appears to exist between spatial attention and eye movements. Indeed, the eyes typically move to the location where attention is allocated, and, vice versa, attention is allocated at possible saccade targets (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). Given the link between working memory and attention, and between attention and eye movements, the question arises as to whether eye movement patterns are affected directly by what one keeps in visual working memory. To address this question, we performed an experiment in which observers had to maintain a location in visual working memory while executing a saccade to another location in space (see Fig. 1).

Previous research has shown that trajectories of saccadic eye movements are often curved away from distractor stimuli that need to be ignored. For example, Doyle and Walker (2001) required observers to execute a saccade in response to a central arrow. On some trials, observers had to ignore a peripheral stimulus that was presented. The results revealed that saccades deviated away from the location of that stimulus. Similar results were reported by Godijn and Theeuwes (2002, 2004) using the oculomotor capture paradigm (cf. Theeuwes, Kramer, Hahn, & Irwin, 1998), in which observers are required to ignore an abrupt onset and to execute a saccade to a color singleton target. When the eyes went correctly to the color singleton target, saccade trajectories deviated away from the location of the onset stimulus. Typically, curvature away from a to-be-ignored stimulus has been attributed to inhibition of stimulus-related activity (e.g., Doyle & Walker, 2001). Because of this inhibition, the overall population of activity generates a saccade vector that deviates away from the location of the stimulus. Thus, previous research has shown that eyes may deviate away from visible stimuli that need to be ignored (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Sheliga, Riggio, & Rizzolatti, 1994). In the present study, we investigated whether a remembered location

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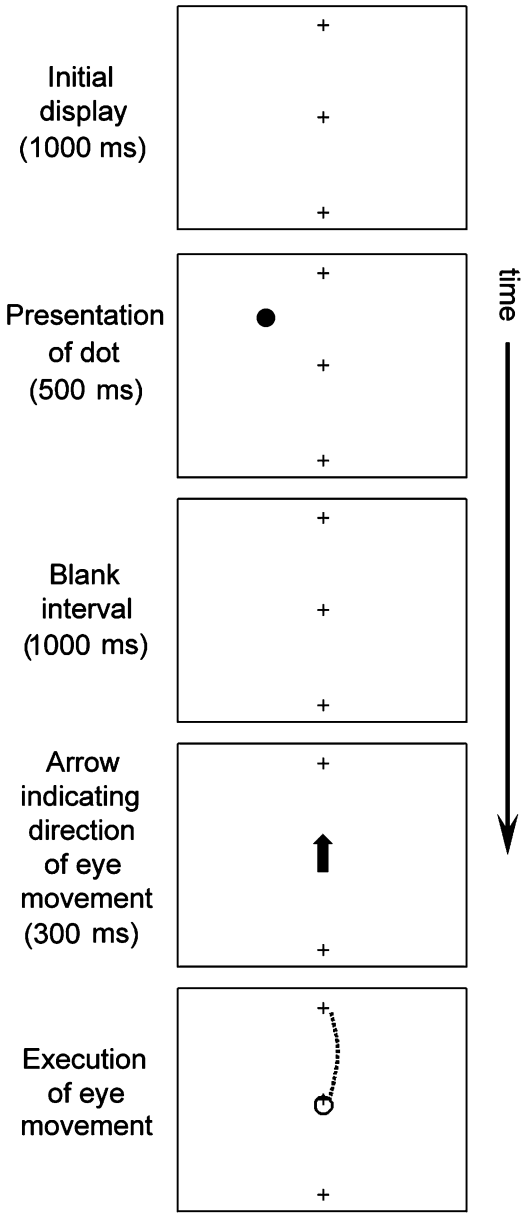

Fig. 1. Typical task sequence. After the initial display, a gray dot was presented somewhere in one of four quadrants. In the memory condition, observers had to remember the location of the dot; in the no-memory condition, observers ignored the dot. After a blank interval of 1,000 ms, an arrow indicated the direction in which a saccade had to be made. The direction of the saccade could be to the same side as where the dot was presented (e.g., upward when the dot was in the top half of the screen) or to the side opposite where the dot was presented (e.g., downward when the dot was in the top half of the screen).

induces a similar deviation. If so, this would provide strong evidence for a direct link between working memory and the oculomotor system.

METHOD

Observers were seated 75 cm from a computer screen with their head positioned on a chin rest. An Eye Link eye-tracking system with a 250-Hz sampling rate recorded eye movements. Observers fixated a center fixation dot (see Fig. 1). After 1,000 ms, a gray dot, 1.35° in diameter, appeared for 500 ms in one of the cells of a 3 × 3 grid (measuring 2.7° × 2.7°) in one of the quadrants of the display (top left, top right, bottom left, bottom right; grids were centered at $x = \pm 5.4°$, $y = \pm 4.9°$ from the fixation point). In one condition, observers had to memorize the location of the dot. In the other condition, the dot was presented but did not need to be memorized. After a blank interval of 1,000 ms, an arrow pointing either straight up or straight down was presented for 300 ms at the center location. Depending on the direction of the arrow, observers immediately made a saccade up or down to a visible marker placed at the top or bottom of the display 6.75° from the central fixation dot.

In the memory condition, the execution of the saccade was followed by a memory test. A white pointer (a ring of the same outer diameter as the dot) was presented at exactly the same location as the initial dot or at a location slightly deviated from the initial location. Observers indicated on the keyboard whether or not the pointer matched the original location.

Each observer performed 144 trials without and 144 trials with the memory task. Order was counterbalanced. Eight observers participated in the experiment.

RESULTS

To determine the effect of the memorized location on saccade trajectory, we calculated the angular deviation of the saccade path for each 4-ms sample point, relative to a straight line from the starting point of the saccade to the saccade endpoint. These deviations were then averaged and collapsed across quadrants (top left, top right, bottom left, bottom right). Figure 2 shows the results normalized onto the top-left location. Separate deviations were calculated according to whether the dot needed to be remembered or not, and according to whether the saccade endpoint and the memorized stimulus were on the same side of the central cross or on the opposite side (i.e., the upper or lower half of the display). Trials on which the initial start or endpoint of the saccade was outside a 3° radius from the designated start and endpoint were excluded from the analysis. This resulted in a loss of 21% of the trials.

An analysis of variance on saccade deviation with eye movement direction (same vs. opposite side of the memorized stimulus) and task (memory or no memory) as factors showed a main effect of direction of eye movement, $F(1, 7) = 13.87$, $p < .01$, $\eta_p^2 = .665$. Also, the Direction × Task interaction was reliable, $F(1, 7) = 7.34$, $p < .05$, $\eta_p^2 = .512$. Deviation away from a straight trajectory was greater when the saccade trajectory passed the to-be-remembered location than when it went in the opposite direction, $F(1, 7) = 3.84$, $p < .01$. Furthermore, the deviation away from a location was stronger when that location had to be kept in memory than when it was simply observed, $F(1, 7) = 2.55$, $p < .05$.

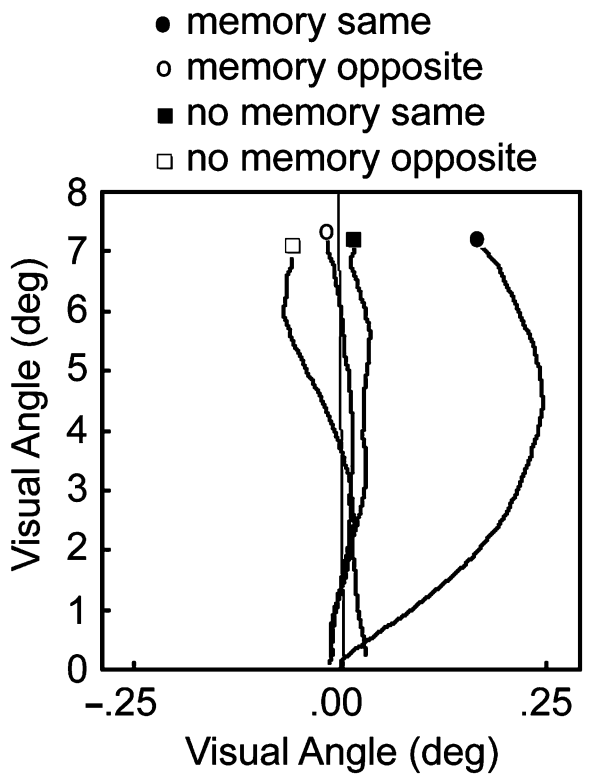

Fig. 2. Eye movement trajectories averaged over observers (collapsed across quadrants and normalized for a dot presented on the left side). Separate trajectories are plotted for saccades going to the same side as the dot or the opposite side, with and without the memory task.

In an additional analysis, memory performance was evaluated. On average, observers made 20.5% errors in the memory task. There was a trend ($p = .16$) to commit more errors when the eyes moved in the same direction as the memorized location (22.5%) than when the eyes moved in the opposite direction (18.6%).

DISCUSSION

Whereas other researchers have demonstrated the close link between visuospatial working memory and spatial attention (Awh & Jonides, 2001; Awh et al., 1998) or between spatial attention and eye movements (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995), here we have shown a direct link between visuospatial working memory and eye movements. More specifically, whereas previous research has shown that the eyes may deviate away from visually presented stimuli that need to be ignored (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Sheliga et al., 1994), we have shown that the eyes also curve away from remembered stimuli.

The current findings provide converging evidence for a strong overlap between visual working memory, spatial attention, and the oculomotor system. A framework for this overlap is provided by the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987; Sheliga et al., 1994). According to this theory, the activation of neural structures related to attention depends on the required motor action. Thus, shifts of spatial attention are considered to be by-products of preparing saccadic eye movements or, in the extreme case, are nothing but such programming of saccades. One important neural structure in this system appears to be the superior colliculus (SC). The SC is a lower-level structure that operates as a motor map for the generation of eye movements; neural activity within the SC encodes the location of a saccade endpoint. The intermediate layers of the SC have direct projections to and from the posterior parietal cortex (Paré & Wurtz, 1997), a region closely related to attentional selection (see Kastner & Ungerleider, 2000, for a review).

Deviations in saccade trajectories have been attributed to competitive interactions of activity within intermediate layers of the SC involved in encoding stimuli as potential saccade targets (Sparks & Hartwich-Young, 1989). Saccade direction is ultimately determined by the mean vector of these activities (Lee, Rohrer, & Sparks, 1988). When a distractor drawing attention is present in the display, its location needs to be suppressed to prevent it from capturing the eyes (Godijn & Theeuwes, 2004). This suppression leads to a shift in the mean vector of activity, resulting in the eye movement deviating away from the distractor (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Sheliga et al., 1994). In this respect, the suppression may be seen as an instance of inhibition of return, the relative slowness of reorienting to a previously attended (and, in the present case, remembered) stimulus (Posner & Cohen, 1984; see also Godijn & Theeuwes, 2004, for the relationship between oculomotor trajectories and inhibition of return). In a study that is also consistent with the inhibition hypothesis, Aizawa and Wurtz (1998) showed similar deviations of saccade trajectories after local inactivation of a region of the SC.

To account for our present findings, we need to extend the premotor theory of attention to include visuospatial working memory. If the process of remembering a certain location is the same as the process of programming an eye movement to that location, remembering a location will generate corresponding activity in the SC. However, note that in our task, observers remember a location to which they are not supposed to make an eye movement. We propose that in order to allow for an accurate saccade to the target location, the oculomotor activity associated with the remembered location in the SC needs to be inhibited. Then, like the inhibition assigned to a visible distractor location, the inhibition assigned to a location in memory causes a saccade curvature away from the memorized location. Thus, memory-based activity can generate competition within the oculomotor system.

The fact that remembered items are represented even at an oculomotor level raises some interesting questions about the nature of memory representations. For one, there is the possibility that working memory is "nothing more" than the preparation to perform an action, whether it be oculomotor, manual,

verbal, or otherwise. Within the premotor theory, the same goes for attention, so the implication is that attention, working memory, and motor preparation should be unified into a single concept. However, if an action then needs to be suppressed (as was the case here), does this mean that the memory itself is suppressed, too? The tendency for participants to make more errors on the memory task when the saccade target and the to-be-remembered location were in the same hemifield than when they were in different hemifields suggests that this may be the case (although there are alternative explanations for this potential difference). Nevertheless, observers still remembered the correct location on the vast majority of trials, indicating that cancellation of an action does not lead to complete cancellation of the memory trace. Instead, there is the possibility that the remembered location is actively represented in higher cortical regions (e.g., the superior prefrontal cortex; Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998), leading to a correct memory representation, but that this location is suppressed in lower regions (in this case, the SC) responsible for the ultimate action. In any case, the present study shows that on the oculomotor level, remembered space behaves like real space.

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